J Comp Physiol A (1991) 169:25–37

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

Action of the octavolateralis efferent system upon the lateral line of free-swimming toadfish, *Opsanus tau*

T.C. Tricas[1,3]* and S.M. Highstein[1,2,3]

[1] Departments of Otolaryngology, [2] Anatomy and Neurobiology, Washington University School of Medicine, 517 S. Euclid Avenue, St. Louis, MO 63110, USA, [3]Marine Biological Laboratory, Woods Hole, MA 02543, USA

Accepted April 29, 1991

Summary. The activation and action of the octavolateralis efferent system was studied by chronic recordings of discharge patterns from putative efferent and single primary afferent neurons in alert, free-swimming toadfish. Efferent axons isolated in the anterior lateral line nerve showed phasic discharges following touch stimuli applied to the head or trunk and demonstrated sustained discharges to visual stimuli. Resting discharge patterns of primary afferents were categorized into irregular, burster, regular, and silent classes. Afferent discharges were often modulated by low frequency (<1 Hz) water movement around the head generated during respiratory movements. When fish with recording electrodes implanted in the lateral line nerve were visually stimulated, modulated peak discharges and average (DC) firing rates were inhibited in irregular-type units only. Inhibition of irregular-type afferent neurons also followed visual presentation of natural prey and persisted long after prey stimuli were removed from view. The inhibitory action upon lateralis afferents when activated by biologically significant visual stimuli leads to the hypothesis that the octavolateralis efferent system functions in the peripheral processing of information carried by the lateral line in natural settings.

Key words: Efferent – Lateral line – Octavolateralis – *Opsanus tau* – Predatory behavior – Vestibular

Introduction

The lateral line of fishes and aquatic amphibians senses hydrodynamic flow near the body surface (Harris and van Bergeijk 1962; Kalmijn 1988, 1989) and functions in schooling behavior (Partridge and Pitcher 1980), localization of underwater objects (van Campenhausen et al. 1981), and prey detection (Hoekstra and Janssen 1985; Montgomery et al. 1988). Hair cells, the transduction elements of the lateral line, are grouped into sensory neuromasts located either upon the skin surface (superficial neuromasts) or enclosed within subdermal canals (canal neuromasts) and provide mechanosensory input to primary afferent neurons of the anterior or posterior lateral line nerves (reviewed in Coombs et al. 1989).

Lateral line primary afferent discharges are modulated by the central nervous system via octavolateralis efferent neurons with cell bodies located in the brainstem and axons that synapse directly upon hair cells (Hama 1965; Flock 1965; Yamada 1973). Electrical stimulation of efferent neurons produces inhibitory postsynaptic potentials (IPSPs) in hair cells and reduces the spontaneous and mechanically evoked discharges of lateralis primary afferents (Russell 1971; Russell and Roberts 1972; Flock and Russell 1976). Octavolateralis efferent neurons are activated by visual, tactile, chemical, vestibular, lateralis, and acoustic stimuli (Klinke and Schmidt 1970; Roberts and Russell 1972; Spätn and Schweickert 1975; Hartmann and Klinke 1980; Highstein and Baker 1985).

One hypothesis for the function of efferent inhibition is to prevent depletion of transmitter from hair cells of the lateral line during locomotion or rapid movements (Russell 1971; Roberts and Russell 1972) but no previous work has investigated the activation or action of the octavolateralis efferent system in natural settings. The neurophysiology and anatomy of the efferent system in the oyster toadfish (*Opsanus tau*) are well studied (Highstein and Baker 1985, 1986; Boyle and Highstein 1990). To address the role of the efferent system in the alert behaving animal, a chronic recording technique was developed that allowed long-term monitoring of single lateral line afferent discharges in the free-swimming toadfish while the efferent system was activated experimentally by visual stimuli including the presentation of natural prey. In these experiments, discharges from only one type of lateral line afferent were found to be inhibited following activation of the efferent system. This action of the efferent system may be important in the peripheral

Abbreviations: *DC* average; *IO* infraorbital; *IPSPs* inhibitory postsynaptic potentials; *MXC* maxillary canal; *OMC* operculomandibular canal; *SOC* supraorbital canal

* Present address: Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, Florida 32901-6988, USA. Send reprint requests to TCT at this address.

processing of biologically relevant stimuli. A preliminary report has been published (Tricas and Highstein 1990).

Materials and methods

Acute experiments. Extracellar recordings were made from axons of the toadfish anterior lateral line nerve. Adult toadfish (20–25 cm total length) were collected near Woods Hole, Mass. USA, lightly anesthetized with methansulfonate (60 mg/l), and immobilized by intramuscular injection of pancuronium bromide (approximately 0.1 mg/kg). Fish were tightly clamped in a small tank filled with seawater to the top of the opercular (gill cover) slit and perfused through the mouth with running seawater. A dorsal craniotomy (4–5 mm diameter) immediately lateral to the sagittal crest of the supraoccipital bone exposed the root of the anterior lateral line nerve. Extracellular recordings were made with glass microelectrodes (2 *M* NaCl, 30–50 MΩ) visually guided to the surface of the nerve. Resting discharges were amplified, filtered, and stored on either analog tape or as discriminated pulse times in digital computer files. Interspike interval histograms were generated off-line to classify the resting discharge patterns of each lateral line afferent.

Chronic experiments. Long-term chronic extracellular recordings from single lateral line primary afferent and efferent axons were made with electrolytically sharpened and insulated (2–5 MΩ) tungsten wire (0.13 mm diameter, 4.0 mm long) mounted in a uniaxial micromanipulator (Fig. 1). The manipulator consisted of a nylon housing (3.0 mm diameter, 11 mm long) threaded at one end to hold a stainless steel screw attached by a ball-and-socket joint to a sliding nylon slug (2.0 mm diameter). The recording electrode was sealed with electrical continuity into a 29G stainless steel tube recessed in the slug face. A 0.18 mm diameter insulated silver wire carried the signal through a guide tube in the wall of the micromanipulator sleeve and exited the skull at the opposite end (Fig. 1).

The identical preparation and surgical procedures described above for acute experiments were used during implantion of the chronic recording micromanipulator (Fig. 2). After exposure of the anterior lateral line nerve and removal of overlying cerebrospinal fluid, a reference wire was threaded through the craniotomy, positioned 1–2 mm away from the recording site, and glued to the skull. The micromanipulator mounted in a holding rod was visually

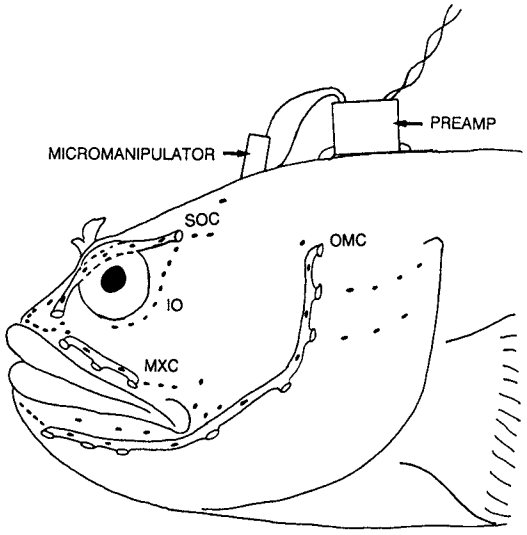

Fig. 2. Distribution of sensory neuromasts innervated by primary afferent neurons of the anterior lateral line nerve in the oyster toadfish, *Opsanus tau*. Canal neuromasts located within the operculomandibular (OMC), maxillary (MXC), and supraorbital (SOC) canals located beneath the skin. Superficial neuromasts are exclusive to the infraorbital (IO) line and are also associated with nerve branches that serve each of the canal organs. Each neuromast is innervated by a unique population of primary afferent neurons, thus stitches apparently do not exist in this species. The mounted micromanipulator and preamplifier used to chronically record from lateral line afferents on the head are also shown

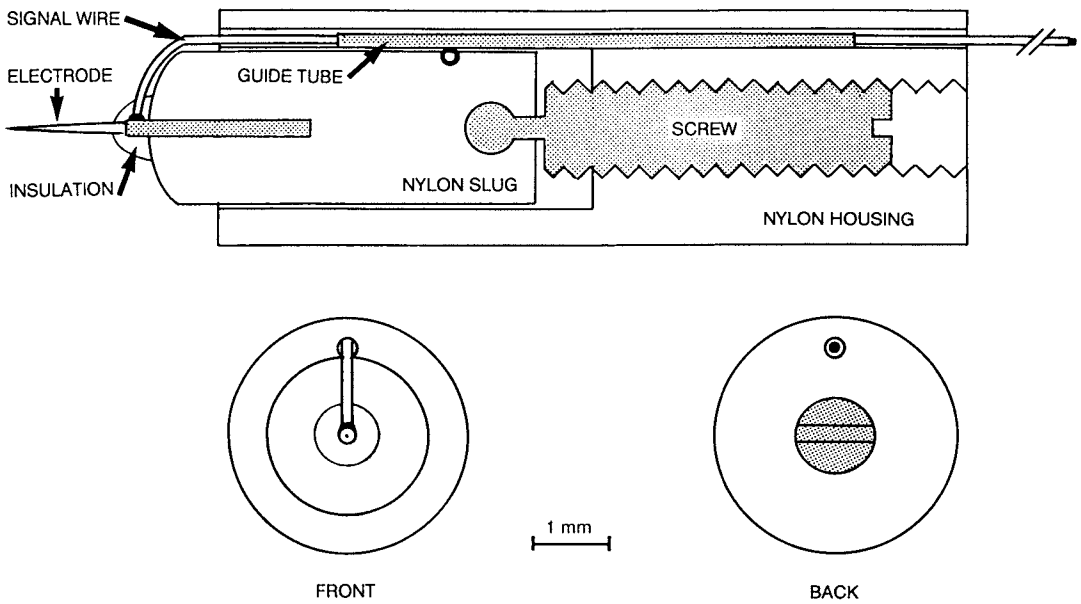

Fig. 1. Micromanipulator used for chronic recordings from single lateral line primary afferents in the oyster toadfish, *Opsanus tau*. The manipulator housing was machined from an 11 × 3 mm nylon rod. A 4 mm tip of an electrolytically etched and insulated tungsten electrode was sealed in a stainless steel receptacle on the face of the moveable slug. The signal lead-off wire carried the analog unit activity from the microelectrode through the manipulator housing wall and out through the back to the preamplifier. The microelectrode could be advanced or retracted along one axis by turning the small screw accessible from the back of the manipulator. Stainless steel components (tubing and screw) are indicated by shaded areas

guided through the craniotomy to the surface of the nerve, glued to the skull with dental acrylic, and released. Cerebrospinal fluid was returned through a small opening that was then sealed, and the muscle and skin sutured in layers. A small potted FET preamplifier (10 mm diameter, 8 mm high, 0.8 g in air, 300-10 kHz bandpass, 100× gain) was sutured on the dorsal midline immediately caudal to the manipulator. The signal and reference wires were soldered to the preamp and sealed with wax. Fine insulated wires (0.5 mm diameter, 1 m long) carried the analog signal to standard amplification, display, and audio monitor equipment. Analog unit data were recorded on one audio track of a stereo video cassette recorder (20–20 kHz bandpass).

After implantation of the chronic recording electrode fish were transferred to an experimental tank (50 × 40 × 15 cm) mounted on a vibration isolation table and supplied with circulating refrigerated sea water maintained at 20–23 °C. Fish exhibited normal swimming, feeding, and aggressive behavior within a few hours following release. Single lateral line axons were isolated by turning the small external screw on the micromanipulator to advance and retract the microelectrode. With this preparation, it was possible to routinely record from single neurons for periods of a few hours to over 2 weeks. During both acute and chronic recording sessions, it was possible to locate and identify the single neuromast innervated by a given afferent by probing the head with a fine jet of water or a 1-mm diameter bead on the end of a fine wire. The ability to identify the specific neuromast that provided input to the unit and the constant profile, amplitude, discharge rate, and interspike interval distribution of the extracellular action potentials were used as the criteria to verify recordings from a single unit for prolonged periods.

Stroboscopic activation of the efferent system. Visual stimuli and light flashes are known to activate fish octavolateralis efferent neurons (Späth and Schweickert 1975; Highstein and Baker 1985; Münz 1985). Multiple stroboscopic bursts (60–100 flashes/s) were administered from above the tank to free-swimming toadfish implanted with the chronic recording electrode. Preliminary experiments showed that these flashes were most effective in dark-adapted fish, thus all animals were maintained in darkness for 15–30 min prior to stroboscopic stimulation. Flash intensity and duration were adjusted to levels subthreshold to those that evoked swimming by the fish (an apparent avoidance response). A video camera (30 frames/s) mounted directly above the tank monitored for any fish movements during all experiments. The toadfish image was magnified so that it filled the monitor screen and maximized spatial resolution of the video system. Because swimming activity produces destructive interactions with mechanical stimuli to lateral line neuromasts that can obscure efferent effects upon afferent activity (Russell and Roberts 1974), only afferent discharge data from experiments in which the toadfish did not move (change position as viewed on video records) following visual stimulation were used. A fiber optic light was used to illuminate the opercular margin in the dark to monitor respiratory activity that modulated the resting discharges of afferent neurons innervating head neuromasts. In some experiments, afferent discharge rates were increased by a low intensity mechanical vibration delivered to the base of the tank with an electromagnetic coil. Stimulus events and analog unit data were recorded on separate audio tracks of the video recorder and analyzed off line.

Visual activation of the efferent system by natural prey. Experiments were performed to test whether visual stimuli naturally encountered by toadfish could influence discharges of lateral line afferent neurons. Toadfish implanted with the chronic recording micromanipulator visually detect, pursue, and readily feed upon small prey introduced into the tank. The killifish (*Fundulus heteroclitus*) is a small natural fish prey for the toadfish (Chrobot 1959) and was used as the prey stimulus in these experiments. To be certain that stimulation of the efferent system was visually-mediated, solitary killifish were enclosed in a clear acrylic chamber (15 × 6 × 4 cm) that was concealed behind an opaque partition positioned in front of the resting toadfish. With this apparatus it was possible to mask chemical, tactile, or local flow field cues that could activate the efferent system through a non-visual sensory modality, and mechanical stimuli that might directly stimulate lateral line neuromasts. Discharge rates of primary afferent neurons were recorded during the 1) prestimulus period as toadfish rested motionless in front of the lowered partition, 2) stimulus period after the partition was raised to present the prey, and 3) poststimulus period after the partition was lowered to again conceal the prey from view. Control experiments that followed the same manipulation protocol but *without* a prey fish in the isolation chamber were performed to test whether the apparatus affected efferent activation or directly stimulated sensory neuromasts. All prey presentation experiments were monitored with the video system as described above, and only data from experiments in which the toadfish did not move towards or strike at prey were used. Data were analyzed separately for efferent action on afferent discharge before, during, and following a predatory strike at killifish prey.

Results

Distribution of head neuromasts

Approximately 122 lateral line neuromasts on the toadfish head are innervated by the two main branches of the anterior lateral line nerve (Fig. 2). Primary afferent neurons in the dorsal ramus of the anterior lateral line nerve receive unilateral excitatory input from the infraorbital, supraorbital, and maxillary neuromast lines. Each infraorbital line is composed of approximately 10 superficial neuromasts positioned ventrolateral and caudal to the orbit. The maxillary line consists of a short canal segment (that contains two neuromasts) located behind the upper lip and adjunct superficial neuromasts at the tip of the snout and upper corner of the jaw. The supraorbital canals are longitudinally positioned dorsal and medial to the orbits, have 5 neuromasts located between two widely separated anterior and caudal pores, and share a short transverse canal segment devoid of sensory neuromasts. Primary afferents of the ventral branch of the lateral line nerve receive input from superficial neuromasts adjacent to and from canal neuromasts within the long operculomandibular tube.

A total of 82 superficial neuromasts are prominently visible on the toadfish head. Each neuromast is positioned between 2 large epidermal papillae that presumably channel water flow over the cupula and contribute to its directional sensitivity (Coombs et al. 1988). It was possible to identify the specific superficial neuromast that provided input to each single primary afferent by probing the neuromast papillae with a fine wire until afferent discharge rates were maximized. All afferent fibers ($n = 160$) encountered during both acute and chronic experiments received excitatory input from a single identified neuromast. Afferent discharges displayed maximal sensitivity to water flow in one direction and could be modulated by an oscillating probe or mild water jet as described for other species (Kroese et al. 1978; Coombs and Janssen 1989; Montgomery et al. 1988). No superficial 'stitches' (multiple neuromasts innervated by a single afferent neuron) were identified on the head of *Opsanus*.

Approximately 28 canal neuromasts located on the head provide mechanosensory input to afferents of the anterior lateral line. Canal neuromasts are enclosed within subdermal membranous tubes some of which are weakly reinforced with cartilage. The locations of individual neuromasts that provided input to primary afferents were identified by mild depression and release of the skin above the canal axis with a fine probe until the phase of discharge ('on' versus 'off') reversed in relation to the applied stimulus.

Resting discharge patterns of anterior lateral line primary afferents

Acute experiments. Primary afferents were classified by their resting interspike intervals in acute experiments on 4 fish. Three discharge patterns were identified among 54 spontaneously active afferent fibers in which spike interval times were recorded. Irregular units (Fig. 3, top) comprised 28% of fibers sampled and innervated both superficial and canal neuromasts. Regular-type fibers (Fig. 3, middle) were rare (5%) and were localized only to superficial neuromasts. Burster afferents (Fig. 3, bottom) had multimodal (usually bimodal) interval histograms, innervated both neuromast types, and were the largest class of fibers (67%) sampled. Silent units were occasionally identified as innervating superficial neuromasts and showed robust, direction sensitive discharges only when the neuromast was mechanically activated by water motion.

Chronic experiments. Forty-seven toadfish were implanted with the chronic recording microelectrode positioned over the anterior lateral line nerve. This nerve has a relatively thin perineurium, thus multiple penetrations of the electrode through the nerve were usually made. In the chronic recording experiments 97 single units were isolated for periods ranging from a few minutes to over 2 weeks. However, the metal microelectrode used in the chronic micromanipulator showed a different sampling bias than that of the glass microelectrode used in acute recording experiments. Irregular afferents were readily isolated with the metal microelectrode while both burst and regular-type units were difficult to isolate and hold for prolonged periods. In the chronic preparation 77% (71/92) of spontaneously active units had irregular discharge patterns while bursters comprised 21% (19/92). Only 2 regular and 5 silent units were identified with the chronic recording system. Figure 4 shows two burst-type afferents recorded chronically in the free-swimming fish. Most bursters had bimodal interspike interval distributions (Fig. 4, top) while only 3 showed multimodal distributions (Fig. 4, bottom). Irregular-type afferents showed typical interspike interval distributions that were strongly skewed to the right (Fig. 5). Unlike recordings from units obtained during acute experiments in which animals were clamped and restrained, resting discharges of almost all afferents in chronic experiments were modulated by direct respiratory motion of the jaw and operculum or associated local flow fields around

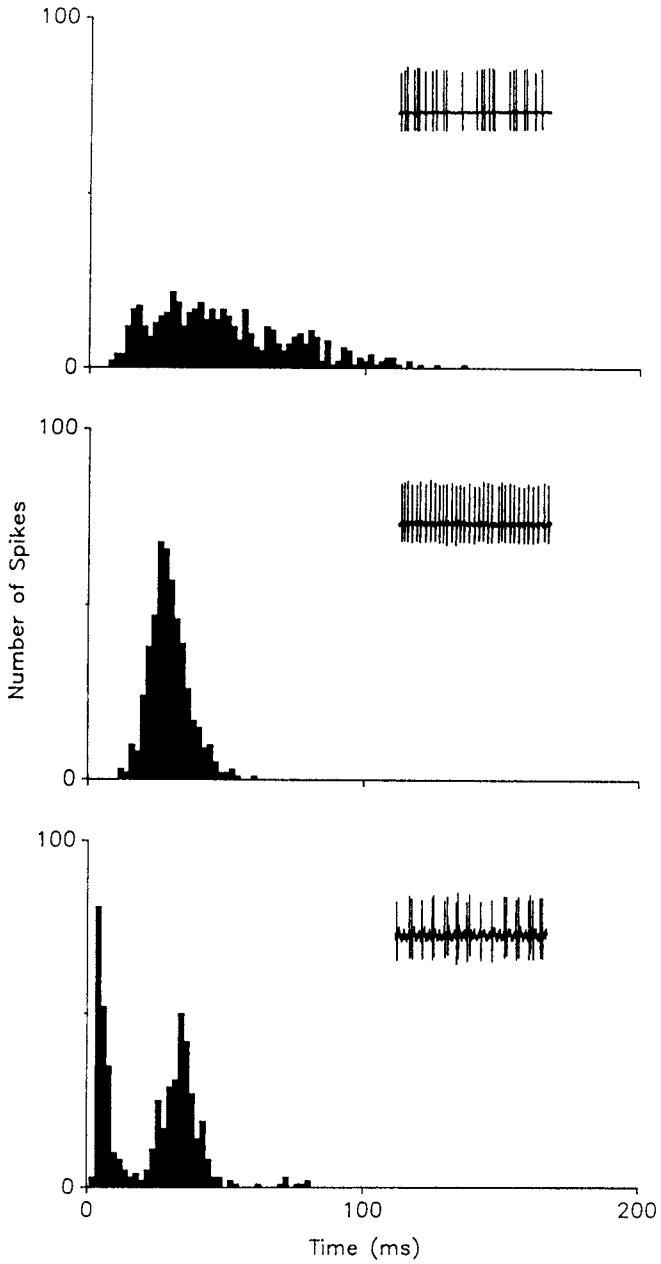

Fig. 3. Resting discharge patterns for 3 classes of primary afferents innervating lateral line neuromasts on the head of the toadfish: irregular (top), regular (middle), burst (bottom). Silent-type primary afferents, which discharged only when the neuromast was mechanically stimulated, were also isolated. Data were recorded in acute experiments and are displayed in histograms of 500 consecutive impulses compiled in 2 ms bins. Insets show analog trace of spike trains recorded for 1 s period for irregular and burst, and 2 s for regular-type afferent

the head. This modulation could be routinely extinguished by restraining opercular movement with a probe.

Discharges of all primary afferent classes isolated in free-swimming toadfish could be increased and entrained in a frequency dependent manner by application of mild sinusoidal vibrations to the base of the experimental tank. Toadfish are negatively buoyant, rest directly upon the substrate when not swimming, and thus move in

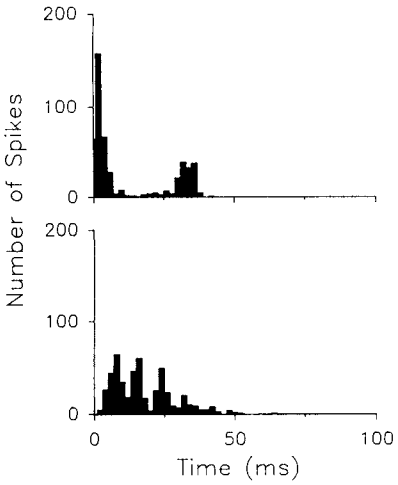

Fig. 4. Resting discharge patterns of burst-type afferents recorded from the anterior lateral line nerve in the free-swimming toadfish. Afferents with burst-type discharge patterns displayed bimodal or multimodal interspike interval distributions. Interspike intervals generated from 500 consecutive spikes and displayed in 2 ms bins

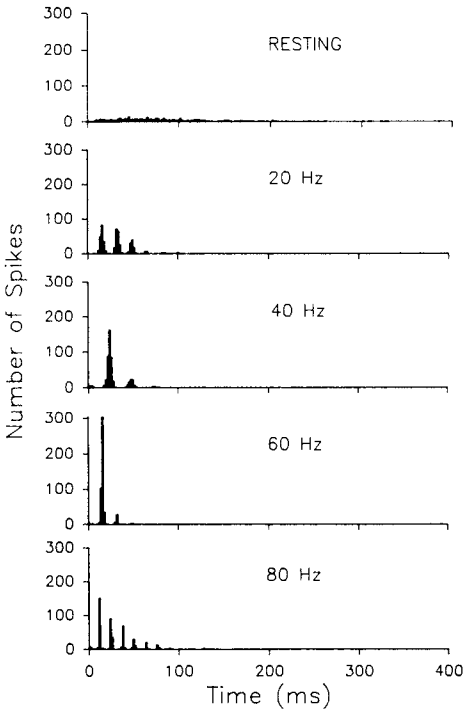

Fig. 5. Discharge patterns of an irregular-type lateral line primary afferent in a free-swimming toadfish stimulated by sinusoidal vibrations applied to the base of the experimental tank. Resting interspike interval histogram shows irregular-type interspike interval distribution. Sinusoidal vibration of tank bottom entrains the irregular-type afferent in a frequency dependent manner. At 20 Hz stimulation, multiple spikes were produced for almost every stimulus cycle. At 40 and 60 Hz the unit was phase locked to the stimulus and discharged nearly every cycle. At 80 Hz the unit remained phase locked, but did not discharge every stimulus cycle. Each interspike interval histogram is composed of 500 consecutive spikes displayed in 2 ms bins. Resting discharge rate of this fiber was 23.8 spikes/s

phase with low frequency substrate vibrations. Motion of the fish skin relative to the surrounding water mechanically stimulates lateral line neuromasts. Broadband vibrational stimuli (containing mixed frequencies) elevated resting rates without changing the firing pattern of irregular units while sinusoidal stimuli altered discharge patterns dramatically. Figure 5 shows the resting discharge pattern of an irregular-type afferent from a superficial neuromast with a resting discharge rate of 23.8 spikes/s that was entrained by a sinusoidal vibration delivered to the substrate. At 20 Hz, the neuron discharged multiple spikes for nearly every stimulus cycle at an average rate of 35.7 spikes/s. At 40 and 60 Hz stimulation, the unit discharge increased to 42.5 and 57.7 spikes/s, respectively, and displayed a single spike for nearly every cycle. At 80 Hz, phase locked discharges increased to 70.2 spikes/s but did not occur for every stimulus cycle. Although stimulus intensity (which undoubtedly influences the degree of phase locking and average discharge rate) was not recorded, these experiments show the toadfish lateral line can encode temporal information about substrate borne vibration.

Efferent activity in free-swimming fish

In previous experiments, it was demonstrated that small bundles of octavolateralis efferent axons can be visually identified and recorded with glass microelectrodes (Highstein and Baker 1985, 1986). These units typically had a low resting discharge rate (5–10 spikes/s) that was often modulated in phase with the respiratory cycle, and showed robust phasic excitation following a light touch to the tip of the snout or surface of the body trunk. During the present chronic recording experiments, 3 units recorded from the anterior lateral line nerve exhibited these characteristics. In distinction to primary afferents, no site of peak sensitivity to mechanical stimulation (i.e. a single neuromast) could be determined for these units. A summary of discharge and response characteristics for one neuron of this type is shown in Fig. 6. The interspike interval distribution of this unit was similar to that of visually confirmed efferent neurons previously recorded (Fig. 6A, cf. legend). As in visually identified efferent neurons, spike discharges recorded in the free-swimming fish were also weakly modulated and in phase with respiratory movements, but showed more noise in their interspike interval distributions. These units also responded with robust phasic increases in discharges to touch stimuli applied over a large area of the head, trunk, and tail (Fig. 6B). After a few hours of behavioral experiments, the free-swimming fish became extremely vigilant towards and sometimes struck at a dark-colored probe as it was moved by the experimenter towards the snout. The approach of the probe elicited a robust and sustained increase in discharge rate (Fig. 6C) similar to that reported for toadfish in acute experiments (Highstein and Baker 1985). No such increase was elicited by a clear glass probe. Although these behavioral experiments support tactile and visually-mediated excitation of efferent neurons, their classification must remain tentative because it was not possible to confirm the central

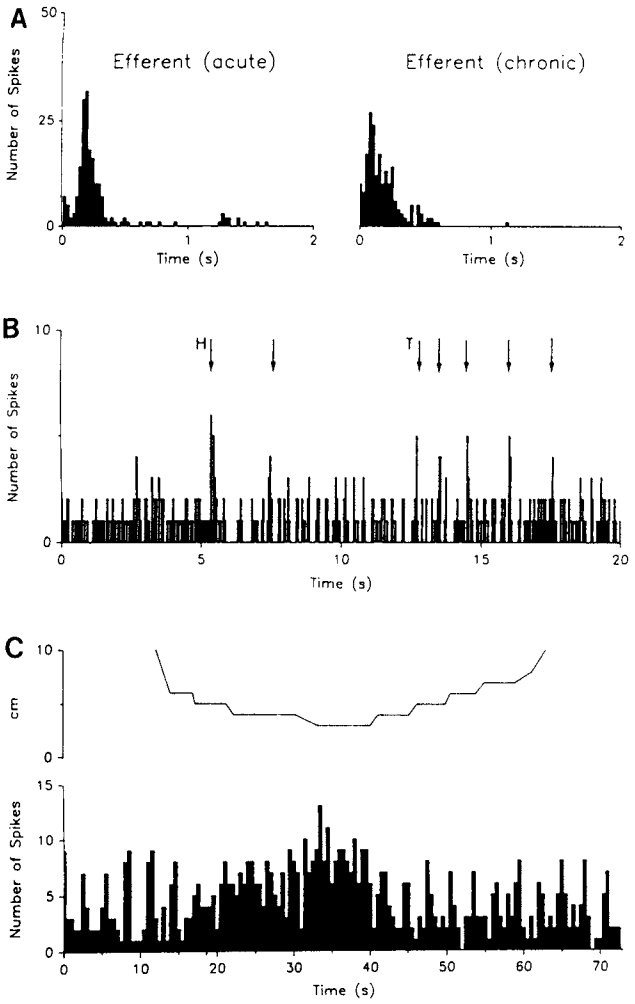

Fig. 6A–C. Single unit recordings from efferent axons in the toadfish. **A** Interspike interval histogram obtained from a visually identified efferent axon during acute experiments (left) is similar to that of a putative efferent neuron chronically recorded in the free-swimming fish (right). Each histogram constructed from 200 consecutive spikes and displayed in 25 ms bins. **B** Phasic discharges from a putative efferent isolated during chronic recording experiments. Unit discharges were evoked by touch of glass probe to the head (H) and surfaces of the body trunk (T). Data displayed in 25 ms bins. **C** Visually-evoked discharges of unit by rostral approach of dark glass probe towards snout during chronic recording experiments. Upper trace: distance of probe from snout throughout experiment. Bottom histogram: efferent discharge increased as the probe was moved towards the eye and decreased when the probe was withdrawn. Similar responses were obtained from lateral approaches on contra- and ipsilateral sides of head. Data displayed in 500 ms bins

origins of these units. Thus, these neurons are classified as putative octavolateralis efferents.

Stroboscopic-mediated inhibition of primary afferent discharges

Flash stimuli decreased lateral line afferent discharges in free-swimming toadfish. The most pronounced decreases were recorded for neurons with discharges strongly modulated by water motion across the operculi during the respiratory cycle at frequencies <1 Hz. Decreases in peak discharge were recorded in 70% (7/10) of irregular-type fibers tested among 6 fish. Decreases in respiratory induced modulation of afferent discharge ranged from less than 10% to greater than 80% of peak discharge rates. Flash trains <5 s duration and spaced 30–60 s apart consistently evoked a decrease in afferent discharges while trains of longer duration (5–15 s) or separated by intervals <5 s evoked an avoidance response in which the fish began to swim around the experimental tank. When dark adapted fish were stimulated with stroboscopic stimuli subthreshold to evoke a swimming response, inhibition of afferent discharge was most prominent during the first few flash trains after which the inhibitory action waned. Figure 7A illustrates this type of response common to all irregular units affected by visual stimulation. Note that the depth of modulation decreased almost immediately following flash train 1, was sustained through flash train 2, but subsequent trains were ineffective. When the afferent discharge rate was increased by introducing a broadband background vibration, both the low frequency respiratory-modulated and broadband evoked discharges were inhibited following stroboscopic stimulation (Fig. 7B). The decrease in the elevated average (DC) firing rate of the primary afferent occurred in 72% (5/7) or irregular units mechanically stimulated by background vibration. Decreased DC discharge rates ranged from 5–30%, but the duration and persistence of the inhibitory response to flashes varied greatly both within and among individual fibers recorded from a single fish. This variation appeared to depend on factors such as the toadfish state of arousal and possible habituation to flash stimuli. No decreases in discharge were detected in 5 burst-type afferents in 5 fish that could be isolated for a sufficient period of time to complete the full experimental protocol. Three of these 5 unresponsive burster units were recorded in the same experimental fish that showed strong inhibition among irregular units. No inhibition was found for 5 additional experiments performed upon burst-type units that could not be held for a complete experiment. Thus it appears that visually-mediated decreases in afferent discharges are restricted to irregular-type units in these behavioral experiments.

Many neuromasts receive natural mechanical stimulation from water flow across the sensory epithelium created during movement of the toadfish respiratory pump. The respiratory cycle of the toadfish begins with enlargement of the buccal cavity and suction of water into the mouth. Expansion of the operculi then draws water from the buccal cavity across the gills and into the parabranchial chamber. Adduction of the operculi and closure of the oral valve forces water out of the parabranchial chamber through the opercular valve. This sequence of respiratory motor movements of the jaw, operculi, and buccal cavity creates water flow external to the head of the alert toadfish at a periodic frequency of approximately 0.2–0.5 Hz.

In all stroboscopic experiments described above, no cessation or reduction of respiratory motion could be observed in video recordings that could account for the

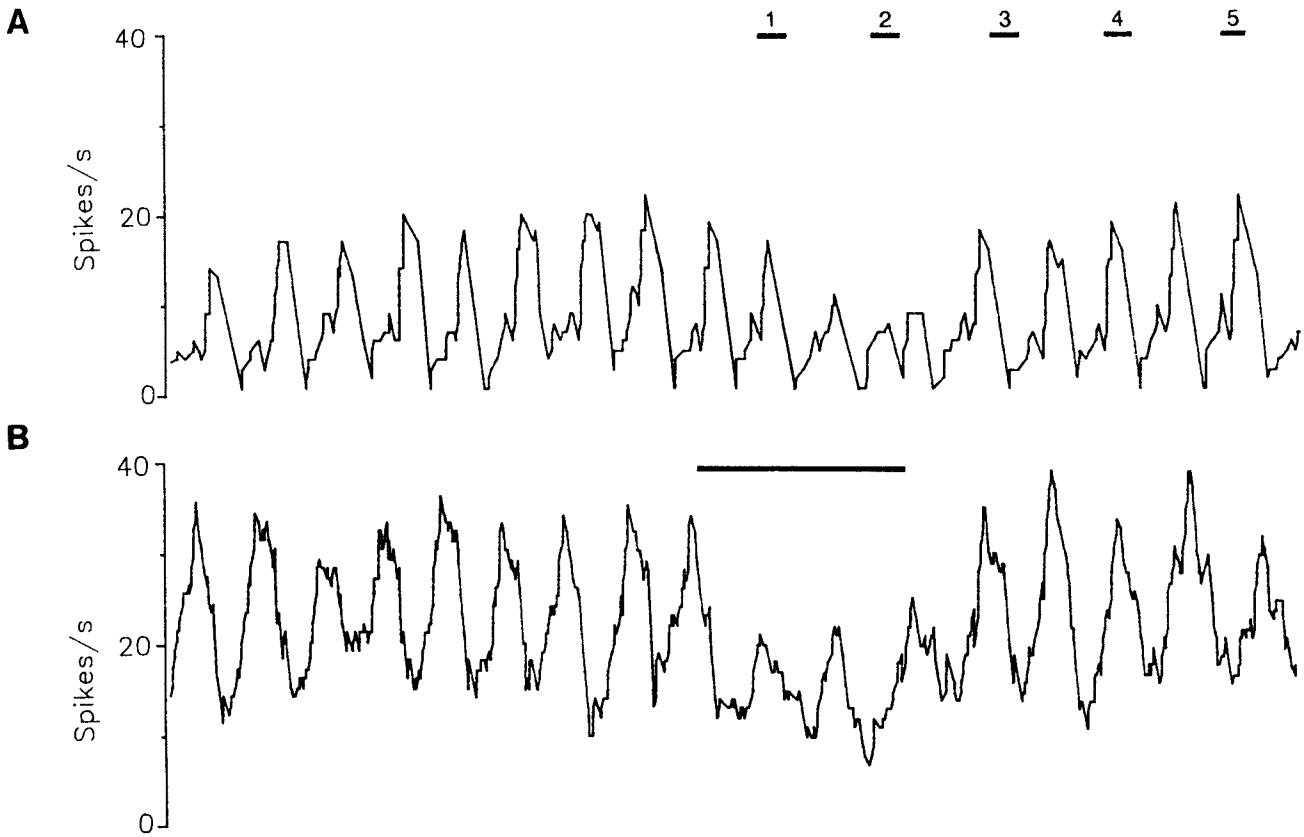

Fig. 7 A, B. Inhibition of an irregular-type primary afferent neuron following stroboscopic stimulation delivered to free-swimming toadfish implanted with the chronic recording electrode. Unit activity is modulated by local water flow around the head generated during respiratory movements. **A** Modulation of neural discharge by low frequency respiratory movement decreases following bright stroboscopic stimulation delivered above the experimental tank. Five individual flash trains (each composed of 100 flashes/s for 1 s duration) are indicated by horizontal bars above trace. Note inhibition was robust after flash trains 1 and 2, but was lacking for subsequent stroboscopic stimuli. **B** Average discharge rate of same neuron was increased by application of a mild broadband vibration applied to the base of the experimental tank. Note that both the average peak discharge that was modulated by the low frequency respiratory stimulus and the average (DC) discharge rate from background noise decreased following a single flash train (100 flashes/s for 8 s period) indicated by horizontal bar across top of trace

decrease in respiratory modulated primary afferent discharges. To further investigate the possibility that a change in opercular movement caused the observed decrease in neural discharge, the opercular margins of 4 experimental fish were monitored with the video camera during the stroboscopic experiments. Figure 8 shows results common to all experiments that confirm the stroboscopically-mediated decrease in discharge were not due to a change in gill motion during the stimulus period. Figure 8A shows a 210 s continuous record of the neural discharges from an irregular afferent that received input from a superficial neuromast located directly upon the operculum monitored. Note that during the 60 s period prior to delivering the first flash train the average discharge rate (39 spikes/s) is stable and evenly modulated by respiratory movements. Following flash train 1, there was a marked disruption of the neural modulation and a 10–15% decrease in the average firing rate to approximately 33 spikes/s (Fig. 8B). As found for all irregular afferents in the stroboscopic stimulation experiments, subsequent flash trains were less effective at reducing the DC discharge rate although both it and the peak modulation remained suppressed for most of the stimulus period. Close-up video records show that the peak excursion of the opercular movements (and presumably other mechanical actions associated with the respiratory pump) were uniform before, during, and following presentation of the stroboscopic stimuli even though discharges decreased in the afferent that innervated this neuromast located on the operculum. Figure 8C shows the magnitude of lateral opercular movements during the stimulus period that generated the modulation of the afferent discharge. Amplitude did not change during the period of inhibition. Thus, the constant amplitude of gill movement indicates the respiratory cycle was neither interrupted nor decreased in amplitude. Since the magnitude of the velocity component of water motion, which is known to be the adequate stimulus to superficial neuromasts (Kalmijn 1989; Coombs and Janssen 1990), is a function of both displacement and frequency, velocities of lateral opercular excursions during the excitatory phase of the afferent discharges were compared for the prestimulus, stimulus, and poststimulus periods. Opercular velocity measured at the lateral margin of the operculum during the expansion phase of respiratory cycle (which was excitatory

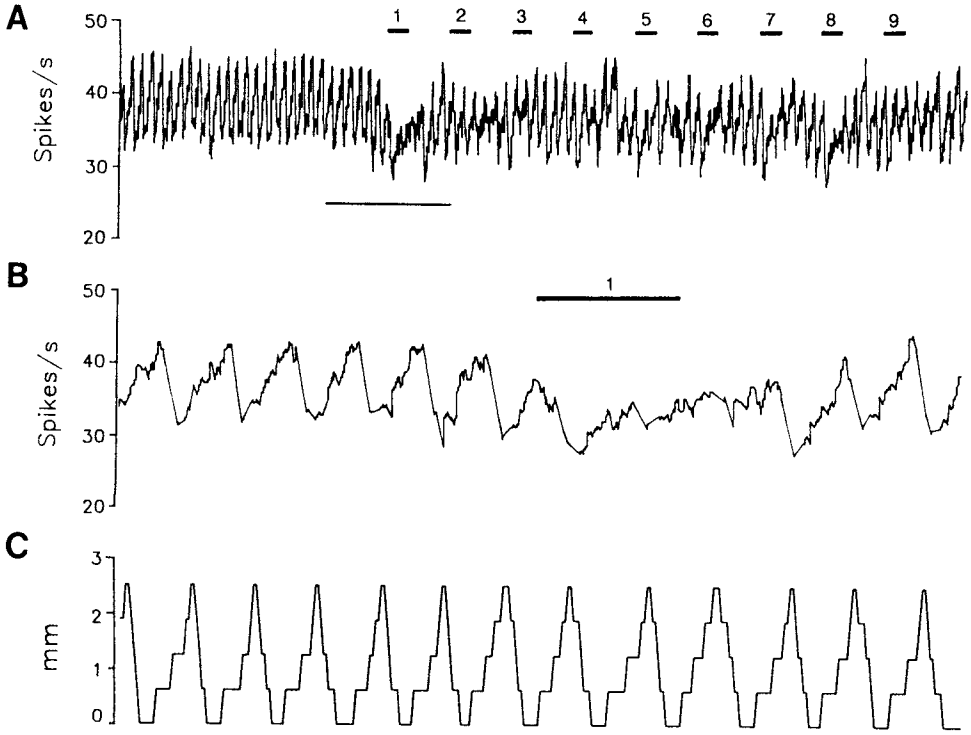

Fig. 8A–C. Stroboscopic-mediated decrease of discharges in an irregular-type afferent modulated by respiratory movements in the free-swimming toadfish. **A** Discharge pattern of lateral line afferent prior to and during 9 stroboscopic flash trains (each delivered at 100 flashes/s for 5 s) shown by solid bars across top of trace. Both peak and unmodulated average (DC) discharge rates decreased. Horizontal bar below trace shows time segment expanded in panel below. **B** Expanded view of afferent discharge during flash train 1 (horizontal bar). Note peak modulation of afferent discharge is reduced following stroboscopic stimulation. **C** Freeze frame analysis of video tape that shows magnitude of lateral displacement of opercular movements during the time segment shown in **B**. Note that opercular displacement remains constant during the stimulation period, thus decreased afferent firing was not due to changes in movement amplitude. Time base and stroboscopic stimulus period are identical to those in **B**

for the afferent) for six cycles during the prestimulus period (2.17 ± 0.25 SD mm/s; $n=6$) did not change for the cycles during observed afferent inhibition or following stroboscopic stimulation (One-way analysis of variance; $F=0.025$; $df=2,9$; $P=0.976$). Thus no change in opercular displacement or velocity that could account for the decrease in neural discharge was detected.

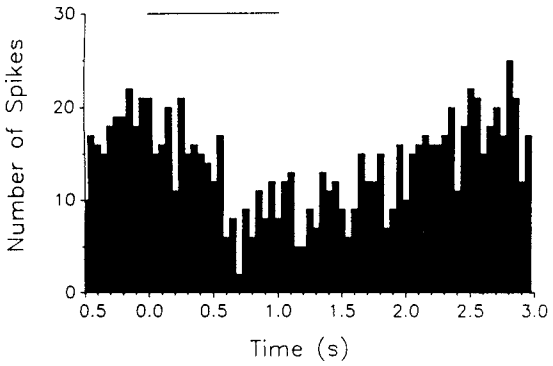

Fig. 9. Peristimulus time histogram that shows latency of inhibitory action of the octavolateralis efferent system upon an irregular-type lateral line afferent neuron following stroboscopic stimulation delivered to a free-swimming toadfish. Histogram shows summed neural response following 10 consecutive flash trains (100 flashes/s, 1 s duration, every 15 s). Note neural discharge showed maximum inhibition approximately 700 ms following onset of stroboscopic stimulus and returns to prestimulus rates approximately 1500 ms after end of stimulus period

The delay between the visual stimulus and recorded decrease in discharge of irregular-type primary afferents is consistent with polysynaptic pathways to the octavolateralis efferent system. The delay to maximum inhibition for the 7 responsive irregular units occurred 350–730 ms following the onset of the stimulus. This latency is demonstrated for one irregular unit in Fig. 9. As described above, inhibition was strongest following the first flash period but was highly variable among subsequent stimulus trains. However, when summed across sequential 1 s flash trains, inhibition appears across the full stimulus period with a poststimulus recovery period of approximately 2–3 s. This latency period is of very similar duration as that recorded for toadfish efferents behaviorally activated in acute bench experiments (Highstein and Baker 1985).

Predatory behavior of the toadfish

Toadfish use an ambush predator strategy to capture small mobile fish prey in the wild (Phillips and Swears 1979; personal observations) but no detailed ethological descriptions of arousal during predation are available. During daylight hours, toadfish rest for long periods

of time directly upon the substrate or positioned near the entrance of a small shelter where they wait for a prey to inadvertently swim within strike range. While the toadfish is at rest, only slight respiratory movements of the operculi and buccal cavity are visible. During the initial phase of arousal when approached by small fish prey, toadfish first erect the soft-rayed second dorsal fin which extends the full length of the trunk. This is followed by flaring of the pectoral and pelvic fins, and occasionally the erection of the small, spiny first dorsal. Under extreme arousal which usually is caused by the close approach of the prey to within a few cm of the snout, toadfish reduce or cease respiratory movements immediately prior to a predatory strike. The strike action pattern consists of a rapid opening of the mouth, expansion of the buccal cavity, and suction of the prey and water into the mouth. Freeze frame analyses of toadfish feeding on *Fundulus* show the entire strike sequence to occur between 65 and 100 ms. After prey capture, water is expelled through the opercular opening and the prey is swallowed.

Visual activation of the efferent system by natural prey

Toadfish implanted with chronic recording electrodes responded to killifish prey swimming in the experimental tank with the typical arousal and strike behaviors seen in wild fish. When prey swam into view, toadfish raised the second dorsal fin. Discharges also decreased in irregular-type primary afferents during this initial phase of arousal. Eighty-eight percent (7/8) of irregular units tested in 5 fish showed decreased average (DC) afferent discharge rates during the period of prey presentation. Although a persistent decrease in unit discharge could be detected, afferent discharge was strongly inhibited both during and following a forceful strike in only 25% (2/8) of tested units (Fig. 10A, vertical arrow). Six irregular afferents were only weakly inhibited during prey presentation and no pronounced inhibition was detected during a strike at the prey. Figure 10B illustrates a representative experiment in which weak inhibition of afferent discharge occurs prior to a predatory strike. Note the epoch of phasic discharge evoked by prey swimming within a few mm of the recorded neuromast (asterisk). Also note that during the strike (vertical arrow) the unit exhibited a very robust increase in discharge activity caused by rapid water movement across the head and neuromast as the toadfish moved to engulf the prey. These data indicate that afferent inhibition during the motor activity of the toadfish strike does not completely inhibit afferent discharges during rapid movement.

Irregular-type primary afferents also showed a strong reduction in discharge rate when *Fundulus* prey were isolated within the visually transparent chamber. A visual stimulus from the prey was sufficient to evoke a decrease in discharges in 83% (5/6) irregular units tested. Figure 11A shows the time course for one complete experiment. As found in the stroboscopic stimulation experiments, the DC discharge rates that were mechanically stimulated by background vibrations decreased during the full stimulus period. However, unlike the short latency to inhibition of afferent discharge found in stroboscopic stimulation experiments, unit discharges were maximally inhibited >10 s after the prey stimulus was presented. Both the intensity of behavioral arousal displayed by the toadfish and onset of afferent inhibition appeared to be enhanced by swimming motions of the prey within the plastic chamber (as contrasted to the prey maintaining a stationary position in the view of

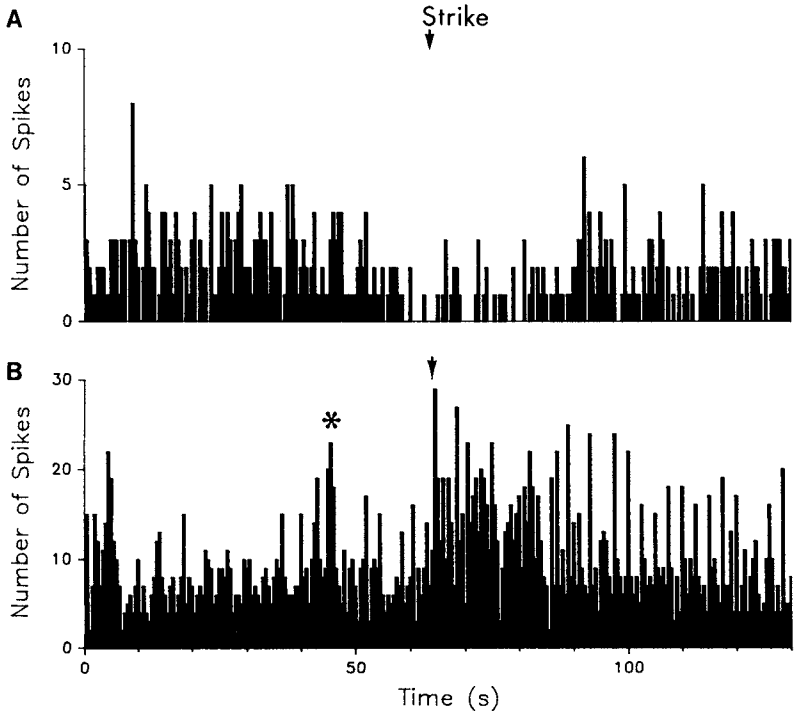

Fig. 10A, B. Discharges of irregular-type primary afferents during presentation of natural fish prey to the free-swimming toadfish. **A** Rare example of afferent in which unit discharge was strongly inhibited prior to, during, and following a strike at the prey (vertical arrow). **B** Discharges of another irregular-type afferent that were modulated during prey presentation, stimulated directly by close approach of prey to neuromast (*), and mechanically evoked by water flow past the head during and following the strike. Most afferents showed responses of this type in which discharges were not completely silenced during prey presentation and were strongly excited by water motion across head neuromasts during a predatory strike

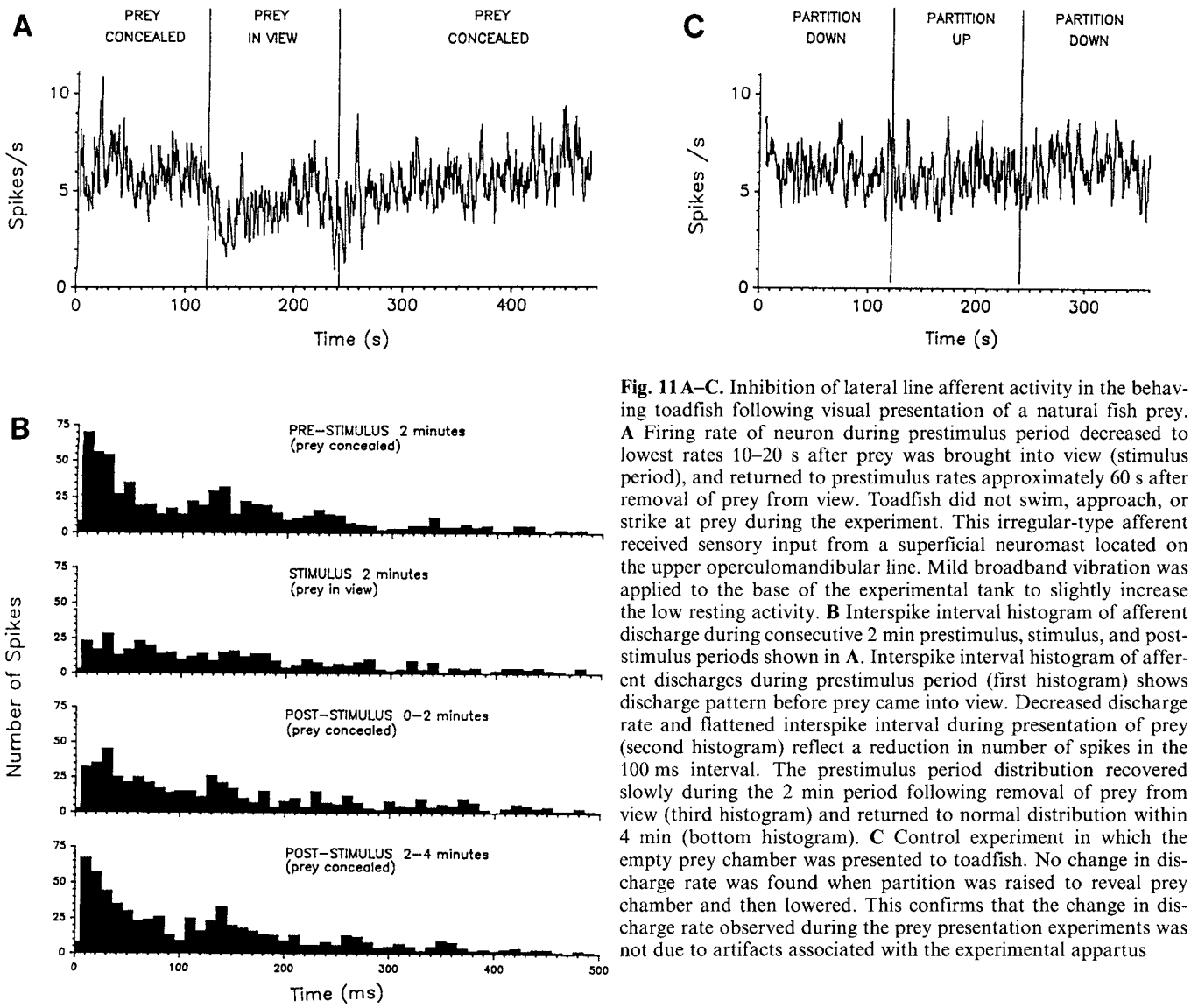

Fig. 11 A–C. Inhibition of lateral line afferent activity in the behaving toadfish following visual presentation of a natural fish prey. **A** Firing rate of neuron during prestimulus period decreased to lowest rates 10–20 s after prey was brought into view (stimulus period), and returned to prestimulus rates approximately 60 s after removal of prey from view. Toadfish did not swim, approach, or strike at prey during the experiment. This irregular-type afferent received sensory input from a superficial neuromast located on the upper operculomandibular line. Mild broadband vibration was applied to the base of the experimental tank to slightly increase the low resting activity. **B** Interspike interval histogram of afferent discharge during consecutive 2 min prestimulus, stimulus, and poststimulus periods shown in **A**. Interspike interval histogram of afferent discharges during prestimulus period (first histogram) shows discharge pattern before prey came into view. Decreased discharge rate and flattened interspike interval during presentation of prey (second histogram) reflect a reduction in number of spikes in the 100 ms interval. The prestimulus period distribution recovered slowly during the 2 min period following removal of prey from view (third histogram) and returned to normal distribution within 4 min (bottom histogram). **C** Control experiment in which the empty prey chamber was presented to toadfish. No change in discharge rate was found when partition was raised to reveal prey chamber and then lowered. This confirms that the change in discharge rate observed during the prey presentation experiments was not due to artifacts associated with the experimental appartus

the toadfish). A strong persistence of afferent inhibition in the highly aroused fish is evident by the long time period (approximately 60 s in this experiment) until discharge rates returned to prestimulus levels after the prey was removed from view (Fig. 11 A). These decreases in afferent discharge involved a marked change in the interspike interval distributions (Fig. 11 B). Following visual presentation of the prey, there was a reduction of spikes within the 100 ms interval (Fig. 11 B, second histogram) which caused the observed decreased discharge rate. The slow recovery is seen during the poststimulus period (Fig. 11 B, third histogram) where the normal afferent discharge pattern remained suppressed for longer than 2 min following removal of the prey from view. Six control experiments in which the empty chamber was revealed to toadfish showed no inhibition of afferent discharge (Fig. 11 C), exclude the possibility of anomalous effects of the experimental apparatus, and support the conclusion that direct visual activation of the efferent system by a natural prey species inhibits afferent discharges.

Similar to the stroboscopic stimulation experiments, there was a decrease in peak discharge of afferents independent of the changes in respiratory activity. Figure 12 presents period histograms of afferent discharge summed over 6 respiratory cycles in the prestimulus and stimulus periods, and compares the peak afferent discharge when gill displacements were of equal amplitudes as monitored on the video tape. Note that peak discharge during the respiratory cycle decreased during the period of prey presentation (Fig. 12, bottom) even though gill movements were of equivalent amplitudes. These experiments indicate that visual stimuli from natural prey also elicit an inhibition of low frequency discharges via the central efferent system that is independent of changes in mechanical stimuli generated by respiratory motion.

Discussion

The gross morphological features of the toadfish lateral line offer distinct advantages for studies of the response

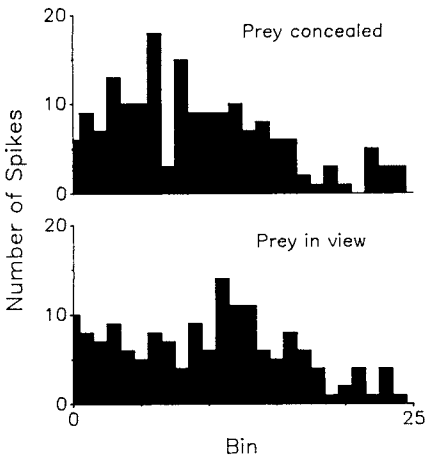

Fig. 12. Period histograms of irregular-type primary afferent discharge during the respiratory cycle prior to and following visual presentation of prey to the toadfish. Upper histogram shows modulation of afferent discharge within respiratory cycles before prey were visually presented (prestimulus period). Note peak discharge occurs during the first 1/2 of the respiratory cycle. Lower histogram shows decreased peak discharge during the normal respiratory cycle when prey was in view (stimulus period). Afferent discharge data pooled from 6 consecutive respiratory cycles for each histogram and displayed in 25 ms bins/cycle. Beginning of each cycle was marked by minimum lateral displacement of operculum. The amplitudes of lateral gill excursions were equal during both the prestimulus and stimulus periods from which the data were analyzed

properties of lateralis afferent neurons. The lateral line in other species studied is composed of hundreds or thousands of small superficial and canal neuromasts arranged in closely juxtaposed branches on the head and trunk often arranged in complex stitches where sensory afferent fibers innervate multiple neuromasts (e.g. Peters 1973; Münz 1979; Coombs and Janssen 1989; Puzdrowski 1989). In toadfish, each of the 82 superficial neuromasts on the head is separated from adjacent neuromasts by relatively large distances (hundreds or thousands of microns) and provide input to a unique set of primary afferents (i.e. no stitches exist in this species). Further, the toadfish lacks scales and each surface pore of the 6 head canal lines can be visually identified and the adjacent neuromasts individually stimulated. These features make the toadfish an excellent candidate for future work to demonstrate any differential response properties of afferents that receive input from superficial vs. canal neuromasts.

The 4 classes of primary afferent neurons (irregular, burster, regular, and silent-type) identified in the toadfish are consistent with discharge properties of afferents reported in other teleost lateralis systems (Münz 1985; Montgomery et al. 1988; Coombs and Janssen 1990). Present results suggest that the discharge properties of burst-type afferents are not due to mechanically evoked artifacts from local oscillations of the recording electrode or background noise as suggested by Wubbels et al. (1990). Irregular and burst-type afferents were isolated in both the acute and chronic recording experiments in which different extracellular methods were used. The isolation of bursters in unrestrained subjects using the short, stout micromanipulator mounted directly to the cranium diminishes the probability that dynamic mechanical deformations of the neural membrane by electrode shaft vibrations cause anomalous burst discharges. Further, these two afferent classes showed differential responses to efferent activation in the behaving animal. All of the above support a distinction between irregular and burst-type afferents in the lateral line in this species.

Activation of the efferent system had a prominent action on irregular-type afferents in chronic experiments. The apparent lack of effect upon burst-type neurons indicates that efferent action differs among afferent fiber classes but the cause of these divergent responses remains unknown. Fiber-dependent ultrastructure features at the periphery such as differential terminal morphology or segregated innervation of hair cells may exist or perhaps efferents project selectively to peripheral hair cells in the sensory neuromast as found in other studies (Flock 1965; Wegner 1982; Highstein and Baker 1986; Meredith and Roberts 1987; Sento and Furukawa 1987). Histological studies where physiologically identified lateral line afferents can be traced to peripheral hair cells and their associated efferent innervation patterns morphologically resolved are needed to address this question.

Activation of the toadfish efferent system is closely associated with arousal behaviors evoked by numerous sensory modalities (Highstein and Baker 1985). When wild toadfish are presented with natural prey, behavioral arousal is progressively expressed by erection of the second dorsal and pelvic fins, elevation of the first dorsal fin, and a reduction or cessation of gilling just before the strike. While there is no doubt that reduction or cessation of gilling in highly aroused fish affects lateral line afferent discharges modulated by respiratory water flow, we have shown that the efferent system also exerts an inhibition of lateral line discharges in the absence of changes in respiratory motor activity. The reduction of the unmodulated average discharge rate following prey presentation and continued suppression long after prey were removed from view strongly support sustained central inhibition of afferent activity.

The sequence of behavioral responses seen during arousal of free-swimming toadfish can also be evoked by graded electrical stimulation of the toadfish efferent nucleus (Boyle and Highstein 1990). Concomitant activation of efferent neurons and muscle systems in other species was demonstrated for non-locomotor muscle activity (Roberts and Russell 1972; Paul and Roberts 1977; Art and Kroese 1982) and locomotor movements (Russell 1971; Schmidt 1963; Klinke and Schmidt 1970). The close association between activation of the efferent and motor systems indicates the octavolateralis efferent system receives significant input from the central nervous system in addition to sense organs of the octavolateralis nerves and was summarized by Roberts and Meredith (1989). However, much work remains to be done to determine the central input pathway to the octavolateralis efferent nucleus and associated motor systems for the toadfish and other anamniotes.

Visually-mediated inhibition in stroboscopic stimulation experiments revealed a latency of approximately 500 ms to maximum inhibition of lateral line afferent discharge. Latencies of a few hundred ms were also reported for toadfish vestibular efferents activated by acoustic, vibrational, mild shock, and touch stimuli (Highstein and Baker 1985) and is consistent with polysynaptic input to the octavolateralis efferent nucleus. In acute experiments, mild touch stimuli delivered to toadfish evoked a robust phasic response by efferents with recovery time constants of 100–600 ms. In that study, efferent discharge rates also increased as a dark glass probe was moved towards the cornea of highly agitated toadfish in a way similar to that found for putative efferents recorded in this study. Although phasic discharges of efferents is a clear response to transient tactile stimulation, sustained elevation of efferent activity that was evoked only in highly aroused fish would be necessary for protracted inhibition of afferent discharge. Latencies to maximum action on vestibular afferents following sustained direct electrical stimulation of the efferent nucleus was approximately 1–2 s (Boyle and Highstein 1990). In the alert, free-swimming fish presented with natural prey, time to maximum inhibition of lateral line afferents was on the order of 10–20 s, and apparently was dependent upon the amount of movement made by the prey. Thus, in biologically relevant contexts the strength and latency to efferent activation is highly variable and may depend upon the stimulus source and motivational/arousal state of the animal.

The octavolateralis efferent system has different actions upon the peripheral end organs of the eighth and lateral line nerves. In the lateral line (Russell and Roberts 1972; Flock and Russell 1973) and saccule (Furukawa 1981) electrical stimulation of efferent neurons is primarily inhibitory upon afferent discharges. In contrast, stimulation of the toadfish efferent system strongly increases the resting discharge rates and dynamic response ranges of high-gain and acceleration sensitive semicircular canal afferents (Boyle and Highstein 1990). In the toadfish lagena, synaptic noise from hair cells is decreased only in irregular-type afferents following stimulation of the efferent nucleus (Locke and Highstein 1990). This differential action of the octavolateralis efferent system upon the different end organs and classes of afferents may function to enhance the central transfer of information from each individual octavolateralis end organ in behavioral contexts which involve high levels of arousal such as predation, courtship, or aggression.

The modulation of afferent discharge by respiratory water flow around the head was strongly reduced by both stroboscopic flashes and visual stimuli from natural prey. Discharges of efferent neurons in the toadfish are also modulated in phase with respiratory activity. Art and Kroese (1982) reported an increase in efferent discharge rate during the respiratory cycle of decerebrate *Xenopus* and concomitant decrease in the spontaneous rate of afferent discharge and sensitivity to mechanical stimulation. These findings indicate that the efferent system may function to reduce the central transfer of very low frequency (<1 Hz) stimuli generated during respiratory movements. However, the spontaneous activity of the octavolateralis efferent system of the toadfish may also exert a centrally biased tonic inhibition upon peripheral lateral line receptors that can modulate receptor sensitivity in the behaving animal. Such a mechanism would account for the upward and downward modulation of resting afferent discharge rates during presentation of natural prey as observed in experiments with the alert, behaving animal.

The results of the chronic recording experiments also bear upon the hypothesis that efferent activation serves primarily to prevent depletion of transmitter from hair cells of the lateral line during locomotion or rapid movements (Russell and Roberts 1972; Flock and Russell 1973). It is significant that neither locomotion, rapid movement, nor any motor activity invariably followed efferent action in the unrestrained behaving fish. Further, afferent discharges due to water movement past the skin were commonly robust when toadfish approached or struck at their prey. Thus, although the Russell and Roberts (1972) hypothesis remains viable, it does not account for the incomplete inhibition during subsequent locomotion or the selective action of the efferent system on lateral line afferents. As described above, it is reasonable to suggest that the efferent system functions to decrease neural input from unwanted mechanical stimuli such as that produced by self-generated respiratory movements. The reduction of DC level discharges induced by broadband experimental background noise indicates the efferent system may also enhance processing of temporal and intensity information from biologically important mechanical stimuli such as that produced by prey near the head and snout. Since burster afferents were apparently unaffected by visual activation of the octavolateralis efferent system in these experiments, the relative input of this class of neurons to central processing regions in the brain may increase during periods of inhibition of irregular-type fibers. Experiments to determine efferent action upon the response dynamics of different lateral line afferent classes and whether differential central projections exist for each cell type will bear upon our hypothesis that efferents function to filter or tune mechanical stimuli at the periphery of this sensory system when activated in biologically relevant contexts.

Acknowledgements. This work was supported by grants from NIH (NRSA and NINCDS) and the McDonnell Center for Higher Brain Function. We thank P. Keller, B. McClure, G. Perry, C. Scudder, A. Steinacker, and T. Warfel for their assistance and S. Coombs for her many discussions during this study.

References

Art JJ, Kroese AB (1982) Effects of efferent activity during respiration on *Xenopus laevis* lateral-line afferent responses. J Physiol 332:21–22

Boyle R, Highstein SM (1990) Efferent vestibular system in the toadfish: action upon horizontal canal afferents. J Neurosci 10:1570–1582

Campenhausen C von, Riess I, Weissert R (1981) Detection of stationary objects by the blind cave fish *Anoptichthys jordani* (Characidae). J Comp Physiol 143:369–374

Chrobot RJ (1959) The feeding habits of the toadfish (*Opsanus tau*) based on an analysis of the contents of the stomach and intestine. MS thesis, University of Maryland, College Park

Coombs S, Janssen J (1989) Peripheral processing by the lateral line system of the mottled sculpin (*Cottus bairdi*) In: Coombs S, Görner P, Münz H (eds) The mechanosensory lateral line. Springer, Berlin Heidelberg New York, pp 299–319

Coombs S, Janssen J (1990) Behavioral and neurophysiological assessment of lateral line sensitivity in the mottled sculpin, *Cottus bairdi*. J Comp Physiol A 167:557–567

Coombs S, Janssen J, Webb JF (1988) Diversity of lateral line systems: Evolutionary and functional considerations. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, Berlin Heidelberg New York, pp 553–593

Coombs S, Görner P, Münz P (eds) (1989) The mechanosensory lateral line: neurobiology and evolution. Springer, Berlin Heidelberg New York

Flock Å (1965) Electron microscopic and electrophysiological studies on the lateral line canal organ. Acta-Otolaryngol, Suppl 199, pp 1–90

Flock Å, Russell IJ (1973) The postsynaptic action of efferent fibres in the lateral line organ of the burbot *Lota lota*. J Physiol 235:591–605

Flock Å, Russell IJ (1976) Inhibition by efferent nerve fibers: action on hair cells and afferent synaptic transmission in the lateral line canal organ of the burbot, *Lota lota*. J Physiol 257:45–62

Furukawa T (1981) Effects of efferent stimulation on the saccule of goldfish. J Physiol 315:203–215

Hama K (1965) Some observations on the fine structure of the lateral line organ of the Japanese sea eel *Lycozymba nystromi*. J Cell Biol 24:193–210

Harris GG, van Bergeijk WA (1962) Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. J Acoust Soc Am 34:1831–1841

Hartmann R, Klinke R (1980) Efferent activity in the goldfish vestibular nerve and its influence on afferent activity. Pflügers Arch 388:123–128

Highstein SM, Baker R (1985) Action of the efferent vestibular system on primary afferents in the toadfish, *Opsanus tau*. J Neurophysiol 54:370–384

Highstein SM, Baker R (1986) Organization of the efferent vestibular nuclei and nerves of the toadfish, *Opsanus tau*. J Comp Neurol 243:309–325

Hoekstra D, Janssen J (1985) Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. Env Biol Fish 12:111–117

Kalmijn AJ (1988) Hydrodynamic and acoustic field detection. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer, Berlin Heidelberg New York, pp 83–130

Kalmijn AJ (1989) Functional evolution of lateral line and inner ear sensory systems. In: Coombs S, Görner P, Münz H (eds) The mechanosensory lateral line. Springer, Berlin Heidelberg New York, pp 187–215

Klinke R, Schmidt CL (1970) Efferent influence on the vestibular organ during active movements of the body. Pflügers Arch 318:325–332

Kroese ABA, van der Zalm JM, van den Brecken J (1978) Frequency response of the lateral-line organ of *Xenopus laevis*. Pflügers Arch 375:167–175

Locke RE, Highstein SM (1990) Efferent modulation of synaptic noise in lagenar afferents of the toadfish. Soc Neurosci Abstr 16:735

Meredith GE, Roberts BL (1987) Distribution and morphological characteristics of efferent neurons innervating end organs in the ear and lateral line of the European eel. J Comp Neurol 265:494–506

Montgomery JC, Macdonald JA, Housley GD (1988) Lateral line function in an antarctic fish related to the signals produced by planktonic prey. J Comp Physiol A 163:827–833

Münz H (1979) Morphology and innervation of the lateral line system in *Sarotherodon niloticus* (L.) (Cichlidae, Teleostei). Zoomorphology 93:73–86

Münz H (1985) Single unit activity in the peripheral lateral line system of the cichlid fish *Sarotherodon niloticus* L. J Comp Physiol A 157:555–568

Partridge BL, Pitcher TJ (1980) The sensory basis of fish schools: relative roles of lateral line and vision. J Comp Physiol 135:315–325

Paul DH, Roberts BL (1977) The location and properties of the efferent neurons of the head lateral-line organs of dogfish. J Comp Physiol 116:117–127

Peters HM (1973) Anatomy and ontogeny of the lateral line system of *Tilapia*, Pisces Cichlidae (Anatomie und Entwicklungsgeschichte des Lateralissystems von *Tilapia* (Pisces, Cichlidae). Z Morphol Tiere 74:89–161

Phillips RR, Swears SB (1979) Social hierarchy, shelter use, and avoidance of predatory toadfish (*Opsanus tau*) by the striped blenny (*Chasmodes bosquianus*). Anim Behav 27:1113–1121

Puzdrowski RL (1989) Peripheral distribution and central projections of the lateral-line nerves in goldfish, *Carassius auratus*. Brain Behav Evol 34:110–131

Roberts BL, Meredith GA (1989) The efferent system. In: Coombs S, Görner P, Münz H (eds) The mechanosensory lateral line. Springer, Berlin Heidelberg New York, pp 445–459

Roberts BL, Russell IJ (1972) The activity of lateral line efferent neurones in stationary and swimming dogfish. J Exp Biol 57:435–448

Russell IJ (1971) The role of the lateral-line efferent system in *Xenopus laevis*. J Exp Biol 54:643–658

Russell IJ, Roberts BL (1972) Inhibition of spontaneous lateral-line activity by efferent nerve stimulation. J Exp Biol 57:77–82

Russell IJ, Roberts BL (1974) Active reduction of lateral-line sensitivity in swimming dogfish. J Comp Physiol 94:7–15

Schmidt RS (1963) Frog labyrinthine efferent impulses. Acta Otolaryngol 56:51–64

Sento S, Furukawa T (1987) Intra-axonal labeling of saccular afferents in the goldfish, *Carassius auratus*: correlations between morphological and physiological characteristics. J Comp Neurol 258:352–367

Spätn M, Schweickert W (1975) Lateral-line efferents to mechanical and visual stimuli. Naturwissenschaften 62:579–580

Tricas TC, Highstein SM (1990) Visual activation of the octavolateralis efferent system during predation in the free-swimming toadfish, *Opsanus tau*. Exp Brain Res 83:233–236

Wegner N (1982) A qualitative and quantitative study of a sensory epithelium in the inner ear of a fish (*Colisa labiosa*: Anabantidae). Acta Zoologica (Stockholm) 63:133–146

Wubbels RJ, Kroese ABA, Duifuis H (1990) Afferent bursting activity of ruff lateral line induced by background noise stimulation. J Comp Physiol A 166:585–588

Yamada Y (1973) Fine structure of the ordinary lateral line organ. I. The neuromast of lamprey, *Entosphenus japonicus*. J Ultrastruct Res 43:1–17